

THE EFFECT OF HERBIVORY RATES ON THE PRODUCTION OF LEAVES AND FLOWERS BY THREE SPECIES OF THE MATORRAL OF CENTRAL CHILE¹

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ABSTRACT

The relationship between herbivory damage and the production of new leaves and flowers in *Quillaja saponaria* Mol., *Escallonia pulverulenta* (R. et P.) Pers. and *Cryptocarya alba* (Mol.) Looser was studied. No relation was found production of new leaves and flowers by the three species and herbivory damage. A multiple regression was significant in *E. pulverulenta*: the number of leaves with galls damage explained 99 % of the variability in the number of flowers. In spite of finding differences between species in the ratio between the number of new leaves and the number of flowers and in the proportion of damaged old leaves, these did not lead to any type of correlation.

Key words: herbivory, vegetative growth, flowering, central Chilean Matorral, *Quillaja saponaria*, *E. pulverulenta*, *Cryptocarya alba*.

RESUMEN

Se estudió la posible relación entre daño por herbivoría y producción de hojas nuevas y flores en *Quillaja saponaria* Mol., *E. pulverulenta* (R. et P.) Pers. y *Cryptocarya alba* (Mol.) Looser. No se encontró relación entre estas variables en ninguna de las tres especies. Una regresión múltiple resultó significativa en *E. pulverulenta*: el número de hojas dañadas con agallas predijo el 99% de la variabilidad en el número de flores. A pesar de que se encontró diferencias entre las especies en la razón hojas nuevas/flores, éstas no fueron significativas.

Palabras claves: herbivoría, crecimiento vegetativo, floración, matorral de Chile central, *Quillaja saponaria*, *E. pulverulenta*, *Cryptocarya alba*.

INTRODUCTION

The transition from the vegetative growth stage to the sexual reproductive stage in the angiosperms is quite dramatic. In the vegetative state, plants continuously generate new leaves, while the switch

to flowering involves a major change in the pattern of differentiation so that the plants must invest generally greater amounts of nutrients and energy (Taiz & Zeiger, 1991). The amount of resources allocated to flower production can be affected by several external and internal factors (Raven *et al.*, 1986). For instance, flower production may be affected by direct attack on flower meristems, or indirectly by defoliation by sap-sucking, skeletonizing, stem-boring and gall-formation (Crawley, 1989, 1997). Severe herbivory during vegetative growth may affect negatively the following flowering process. Such damage may imply lower photosynthetic surface, thus affecting directly energy intake. Damage may also induce the production of costly defences and/or the allocation of resources to tissue reparation, which in turn may reduce the plant budget allocated to flowering.

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The Chilean central 'matorral' (Montenegro *et al.*, 1989) is occupied by species which develop under different herbivory exposure through the year and are thus affected in different scales and ways (Fuentes *et al.*, 1981). In the present work, a study was undertaken of the effect of damage due to past herbivory on the production of new leaves and flowers in three matorral species.

METHODS AND MATERIALS

Sampling was carried out in the Río Clarillo Natural Reserve (33°51'S, 70°29'W, 45 km southeast of Santiago, Chile). Two hundred grams of branches of *Quillaja saponaria* Mol., *E. pulverulenta* (R. et P.) Pers. and *Cryptocarya alba* (Mol.) Looser were collected, with 10 replicates for each species. The number of old and new leaves with and without damage was recorded as well as the number of flowers (buds and mature flowers). The damage in old and new leaves was classified according to different types of herbivory: chewing, sap-sucking, skeletonizing and gall-forming.

The existence of a relation between herbivory of old leaves and the production of new leaves or new flowers, Spearman rank correlations were performed for each tree species. Multiple regressions were also used to identify any tendencies in flower and leaf production in relation to previous herbivory.

RESULTS

In *Quillaja saponaria* the total number of new leaves was higher than both the number of old damaged leaves and the total number of flowers. Contrastingly, in *E. pulverulenta* there was a lower

number of vegetative structures and similar number of flowers as in *Q. saponaria*. *Cryptocarya alba* had a very small number of flowers and a higher number of old and new leaves with and without damage (Figure 1).

Chewing damage was the most frequent type in *Q. saponaria*, and was far more frequent than all other types of damage. In *E. pulverulenta*, damage levels were very low and no marked differences existed between damage types. In *C. alba*, sucking and chewing were the most frequent damage types and all other damage types were negligible (Figure 2).

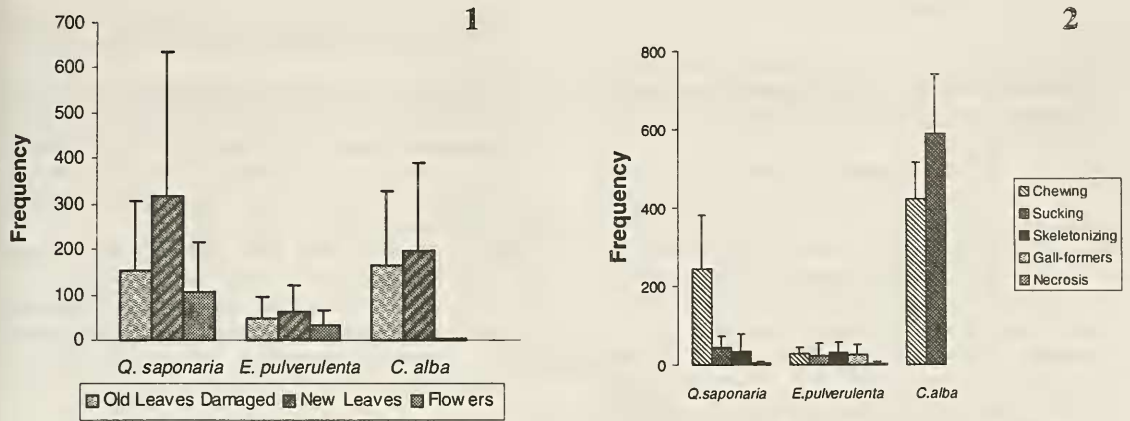
Only in *Q. saponaria* there was a negative correlation between the number of total new leaves and the number of old leaves with damage ($r_s = -0.66$; $P = 0.04$). A multiple regression to assess the relative importance of different types of damage on new leaf production (using frequency of new leaves as a dependent variable and frequency of each type of damage on old leaves as independent variables), gave no significant correlations in any of the species studied. However, when flower frequency was used as the dependant variable a significant correlation ($P < 0.0001$) was found in *E. pulverulenta*; in this case, the number of gall-damaged old leaves explained 99 % of the variability in flower frequency. No other significant correlations were found with any of the other species (Table 1).

Significant differences were found between species in the number of new leaves / number of flowers ratio ($F_{2,27} = 15.53$; $P = 0.00003$; one-way ANOVA). Through Tukey multiple range test ($P < 0.05$), significant differences were found between *C. alba* and the other two species, *C. alba* exhibiting the highest ratio. The same was true for the proportion of damaged old leaves between species

TABLE I
SUMMARY OF REGRESSION ANALYSIS. DEPENDENT VARIABLE: NUMBER OF FLOWERS; INDEPENDENT VARIABLES: NUMBER OF OLD LEAVES WITH DIFFERENT TYPES OF HERBIVORY

	Beta	St. error of Beta	B	St. error of B	t(6)	P-level
Intercept			1.911	6.778	0.282	0.787
Chewing damage ^a	0.146	0.078	0.303	0.161	1.879	0.109
Sucking damage ^a	0.057	0.079	0.067	0.091	0.732	0.491
Gall damage ^a	0.998	0.079	1.289	0.102	12.57	0.000015

^aNumber of old leaves with stated type of damage



Figures 1-2. 1. Number of damaged old leaves, new leaves, and flowers in *Quillaja saponaria*, *Escallonia pulverulenta*, and *Cryptocarya alba* 2. Damage type in old leaves of *Quillaja saponaria*, *Escallonia pulverulenta*, and *Cryptocarya alba*

($F_{2,27}=131.74$, $P < 0.0001$; one-way ANOVA). In this case, three different groups were found through Tukey multiple range tests ($P < 0.05$), where *Q. saponaria* presented the highest proportion of damaged old leaves, followed by *E. pulverulenta* and *C. alba*.

DISCUSSION

In none of the species studied there was evidence of a relationship between the number of leaves per flower produced by the plant and herbivory of the old generation of leaves in these species. Such relation was expected since it has been suggested that there are direct and indirect effects of old herbivory on the general performance of a plant (Crawley, 1989; Waterman & Mole, 1989), its vegetative growth (Quiring & McKinnon, 1999), its reproductive success (Crawley, 1989) and the final decision of the plant to choose the developing course of their meristems and buds (Crawley, 1997). All these factors seem to be conditioned by external and internal factors, besides the herbivory, as has been reported in other species (Waterman & Mole, 1989). The present results should be taken cautiously because of the limitations of the sampling period.

Despite this limitation, the present results suggest that for *Q. saponaria* and *C. alba* damage due to past herbivory does not affect subsequent vegetative growth and flowering. This may indicate that the

assumption of trade-off underlying the pattern of energy allocation in plants does not hold. Thus, in these species damage does not imply decreasing allocation to flowering. On the other hand, availability of resources to life history demands may not be limiting in these cases. Further studies are needed in order contrast these hypotheses.

E. pulverulenta showed a positive correlation between damage in old leaves by gall-formers and the number of flowers produced. This suggests that not only the assumption of trade-off underlying the pattern of energy allocation in the plant does not hold, but a possible mechanism of flowering induced by galling may be occurring.

The fact that *C. alba* showed more flowers per old leaf than the other species may be attributed to a delay in the flowering of this species during the present season.

Future work should address how damage affects photosynthetic capacity of tissues (i.e. to look at area damaged instead of frequency of damaged leaves), and carry out evaluations in different time and space coordinates, as well as incorporating experiments with artificial damage.

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LITERATURE CITED

- CRAWLEY, M. 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. *In*: E. Bernays (ed.), *Insect-Plant Interactions*, vol. 1, pp. 45-72. CRC Press, USA.
- CRAWLEY, M. 1997. Plant-herbivory dynamics. *In*: M. Crawley (ed.), *Plant Ecology*, 2nd ed., pp. 401-474. Blackwell Sciences, Australia.
- FUENTES, E. R., ETCHEGARAY, J., ALJARO, M.E. & MONTENEGRO, G. 1981. Shrub defoliation by matorral insects. *In*: di Castri, F., D. W. Goodall & R. Specht (eds.), *Mediterranean-type shrub lands*, pp. 345-359. Elsevier, Amsterdam.
- MONTENEGRO, G., AVILA, G., ALJARO, M.E., OSORIO, R. & GÓMEZ, M. 1989. *In*: G. Orshan (ed.), *Plant pheno-morphological studies in mediterranean type ecosystems*, pp.347-387. Kluwer Academic Publishers. Netherlands.
- QUIRING, D. T. & MCKINNON, L. 1999. Why does early-season herbivory affect subsequent budburst? *Ecology* 80: 1724-1735.
- RAVEN, P., EVERT, R. & EICHHORN, S. 1986. *Biology of the plants*. 4th ed. Worth Publishers, Inc. New York.
- SOLERVICENS, J., ESTRADA, P. & MÁRQUEZ, M. 1991. Observaciones sobre entomofauna de suelo y follaje en la Reserva Nacional Río Clarillo, Región Metropolitana, Chile. *Acta Entomológica Chilena* 16: 161-182.
- TAIZ, L. & ZEIGER, E. 1991. *Plant physiology*. The Benjamin/Cummings Publishing Company Inc., California.
- WATERMAN, P. & MOLE, S. 1989. Extrinsic factors influencing production of secondary metabolites in plants. *In*: E. Bernays (ed.), *Insect-Plant Interactions*, vol. 1, pp. 107-134. CRC Press, USA.